

Invited article**Major Evolutionary Advances in the History of Green Land Plants¹****KLAUS KUBITZKI***University of Hamburg, Germany*

The emergence of terrestrial plant life about 500 m ys ago is testified by liverwort-like and later moss-like tissue fragments consisting, *i.e.*, of sporopollenin-containing spore walls and waxy cuticles. Macrofossils from the Early Devonian represent low patch-forming land plants that retained bryophyte-characteristics but had branched sporophytes and contained VA-mycorrhiza-like endophytes. Impregnation of cellulosic cell walls by lignin made possible the construction of larger plant bodies exploiting the light/air-space. At the same time the earliest lycophytes appeared, documenting the split of this lineage from the line leading to the remaining green land plants. In the Late Devonian progymnospermous trees appeared in which pseudomonopodial branching was superseded by lateral branching. The acquisition of the seed habit in the seed fern lineage was probably followed by the still problematic transition from the homorhizic pteridophyte organisation to the allorhizic seed plant organisation, the latter also implying axillary branching. During the Carboniferous, in different lineages strange tree constructions evolved, deriving mechanical strength from root mantles, tubular stems, or periderm tissue, yet nearly all of these lineages, at latest by the Permian, succumbed to the shrinking of wetland habitats. The interval from Permian to Mid Cretaceous was mainly a period of variation of the gymnosperm theme, with the rise and demise of several seed fern and other gymnospermous groups. It is most probable that the rise of the angiosperms was mainly due to their flexible developmental system, which permitted, *i.e.*, the evolution of short-lived herbaceous plant bodies and "cheap" seeds.

The phenomenon of "unequal split", *i.e.*, the difference in number of taxa between sister groups, leads to the notion that evolutionary success is hardly predictable. Instead, evolutionary success seems to depend on the coincidence between the accumulation of interactive traits in a lineage and a benign constellation of environmental opportunities. This is exemplified by the spread of modern filicalean ferns, which diversified during the Cretaceous in the shadow of the angiosperms.

Key words: allorhizy, axillary branching, green land plants, heterospory, lignin, root mantle trees, seed habit

Land plant beginnings

In the history of earth, the emergence of terrestrial plant life was the start of unparalleled diversification

and innovation, yet the first evidence, dating back to nearly 500 m ys, is modest; it consists of spore tetrads with a decay-resistant wall, and fragments of cuticles, which appear over a broad geographic

¹ I gratefully dedicate this paper to my distinguished colleagues K. Iwatzuki, M. Kato, M. Tamura, M. N. Tamura, H. Tobe, and H. Ohba, who were contributors to or referees for my book series "The Families and Genera of Vascular Plants".

This article is formed from the presentation as one of contributions for the International Symposium 2004, Asian Plant Diversity and Systematics, held at Sakura, Chiba, Japan on July 29 - August 2, 2004.

area in the mid-Ordovician. These fossils suggest a land vegetation of liverwort-like plants. In the Silurian, tetrads began to decline in diversity and were largely replaced by individually dispersed spores probably produced by hornwort and moss-like land plants. Early innovations testified by these plants include sporopollenin-impregnated spore walls, waxy cuticles, and simple water-conducting tissues of the kind that exist in extant mosses, all being clear responses of aquatic plants to the new, aerial environment (see Kenrick & Crane 1997).

In the Early Devonian archaic land plants such as *Aglaophyton* (former *Rhynia major*) and *Horneophyton* appeared that shared several features with bryophyte sporophytes, including terminal sporangia, the lack of leaves, roots and tracheids (and lignin, by that way), but were innovative in having a branched, nutritionally independent sporophyte and harbouring VA-mycorrhizal-like endophytes in their rhizomes (Wilkinson 2001, Brundrett 2002). They spread vegetatively by growth of prostrate axes, which formed monospecific patches. Their tufts of rhizoids at the lower surface of their horizontal axes had a limited capacity to penetrate the substrate to acquire water and nutrients. Since flavonoids are known from extant bryophytes and also from the charalean stock, which was ancestral to green land plants (Markham & Porter 1969), we can safely assume that these compounds, which are a common UV screen in the epidermises of extant tracheophytes, acted the same way from the beginnings of land plant evolution.

In the Rhynie chert beds of Scotland, *Aglaophyton* co-occurred with the famous *Rhynia gwynnevaughanii*. The important advance of *Rhynia* was the water conducting system with tracheids, which owed their rigidity to impregnation with lignin. The encrustation of cellulosic cell walls with lignin

allowed the construction of large plant structures capable of exploiting the light/air space and thus became of greatest importance for the conquest of the land surface. What is so remarkable is that lignin is solely based on phenylpropanoid moieties - all lignin of one large tree individual is but a single macromolecule!

At about the same time, early zosterophylls and particularly the strange *Baragwanathia*² testified the appearance of the lycopodian lineage, which represents the first split from the remaining tracheophyte lineage, confirmed by numerous morphological innovations (Kenrick & Crane 1997, Schneider *et al.* 2002) and an ancient split in plastid DNA (Raubeson & Jansen 1992).

In the Early and Middle Devonian terrestrial plant communities were probably quite simple in structure and dynamics and consisted of an array of patches usually dominated by a single species, and much unoccupied space on the land surface provided ample evolutionary opportunities. At that time rhyniopsids, zosterophylls, lycopsids and trimerophytes became important and brought morphological innovations such as pseudomonopodial axes with main trunks and secondary vascular tissues, permitting the build-up of taller plant bodies. In the Middle Devonian, trimerophytes reached a size of up to 2 m but in spite of thick axes are not known to have had roots. Lycopsids such as *Asteroxylon* developed aerial axes borne on rhizomes that produced forked roots, thus supplementing and amplifying anchorage and absorptive capacities. Now increasingly subsurface water and nutrients could be utilized, which permitted the colonization of slightly drier habitats.

First tree forms, and evolution of the seed habit

² *Baragwanathia* had, for a long time, been accepted as the earliest, Silurian, land plant but more recent evidence places it in the Early Devonian. Also the Silurian age of the famous *Pinnatiramosus* (Geng 1986) is contentious (see Edwards 2001).

In the Late Devonian a dramatic increase in species richness and morphological modernisation of the flora took place. The progymnosperms combined massiv, conifer-like stems with fern-like foliage and free-sporing homosporous or heterosporous reproduction. *Aneurophyton* was protostelic but had secondary wood and periderm and large appendages, which probably were formed by pseudomonopodial branching and cannot clearly be designated as branches or fronds. Towards the end of the Devonian various species of *Archaeopteris* became dominant forest trees in floodplains; their eustelic axes reached to 10 m in height and 1.5 m in diameter and apparently for the first time possessed some kind of lateral branching (Meyer-Berthaud *et al.* 1999), by which the risk of damage to the trunk apex could be overcome. They were provided with distal dichotomising and three-dimensional, not planated branching systems, which in some species graded into leaves. The progymnosperms were homosporous or heterosporous, but in the Late Devonian, and increasingly in the Early Carboniferous, the spread of the seed habit allowed the invasion of upland habitats. The seed ferns were superficially similar to progymnosperms in having large fronds crowded at the apex of the stems, but apart from thick-stemmed forms also climbers and elegant treelets provided with stilt-roots appeared. By the Early Carboniferous seed ferns had become important elements of the land surface.

The evolution of the seed habit was probably the most important innovation in the history of land plants. It was initiated by the transition from homospory to heterospory, which occurred independently in at least eleven lineages of tracheophytes (Bateman & DiMichele 1994). In most of them, this initial step was followed by dioecy and heterosporangy, while endospory and reduction to a single megaspore, which remained included in the megasporangium and enclosed in an integumentary envelope, was, apart from the seed plant lineage, only attained in the Lepidodendrales. The advances from

incipient heterospory to the production of seeds occurred in the Upper Devonian during a time span of only 40 m ys. The adaptive break-through made by the seed plants implied the effective transfer of the male gametophyte to the female independently from a fluid medium, and the young sporophyte (embryo) became capable of resisting desiccation and cold. One may ask, what might have been the advantage for the lineages in which the sequence of innovations of the reproductive system stopped at the stage of heterosporangy or endomegasporangy, without leading to the seed habit? Homosporous embryophytes, such as nearly all extant pteridophytes, have a biphasic life cycle, in which the sporophytic phase can invade drier habitats than the gametophytic phase, which depends on water as the medium for sperm transfer. In other words, both phases depend on the same genome but may have different ecological preferences and then are subject to different selective forces. In contrast, with the acquisition of endospory the increasingly dominant sporophyte becomes the principal target for selection (Bateman & DiMichele 1994), and the life cycle is more unified.

Evolution of seed plant organisation

Apart from the ecological advantage of the seed habit, the structure of the embryo went through a profound transformation on its way from the pteridophytic to the spermatophytic stage. In (extant) pteridophytes the embryo has only a shoot apex and thus is unipolar, and the first and all further roots are lateral, developing endogenously and in conjunction with the leaves; a root system proper is lacking (Fig. 1 A, B). The seed plant embryo, being immersed into the endosperm by the elongating suspensor, appears bipolar³ with the shoot meristem opposed to the radicle, from which a primary root develops, which is capable of building up a root system (Fig. 1 C-E). Polarity seems to be imprinted upon the embryo by the female gametophyte, as

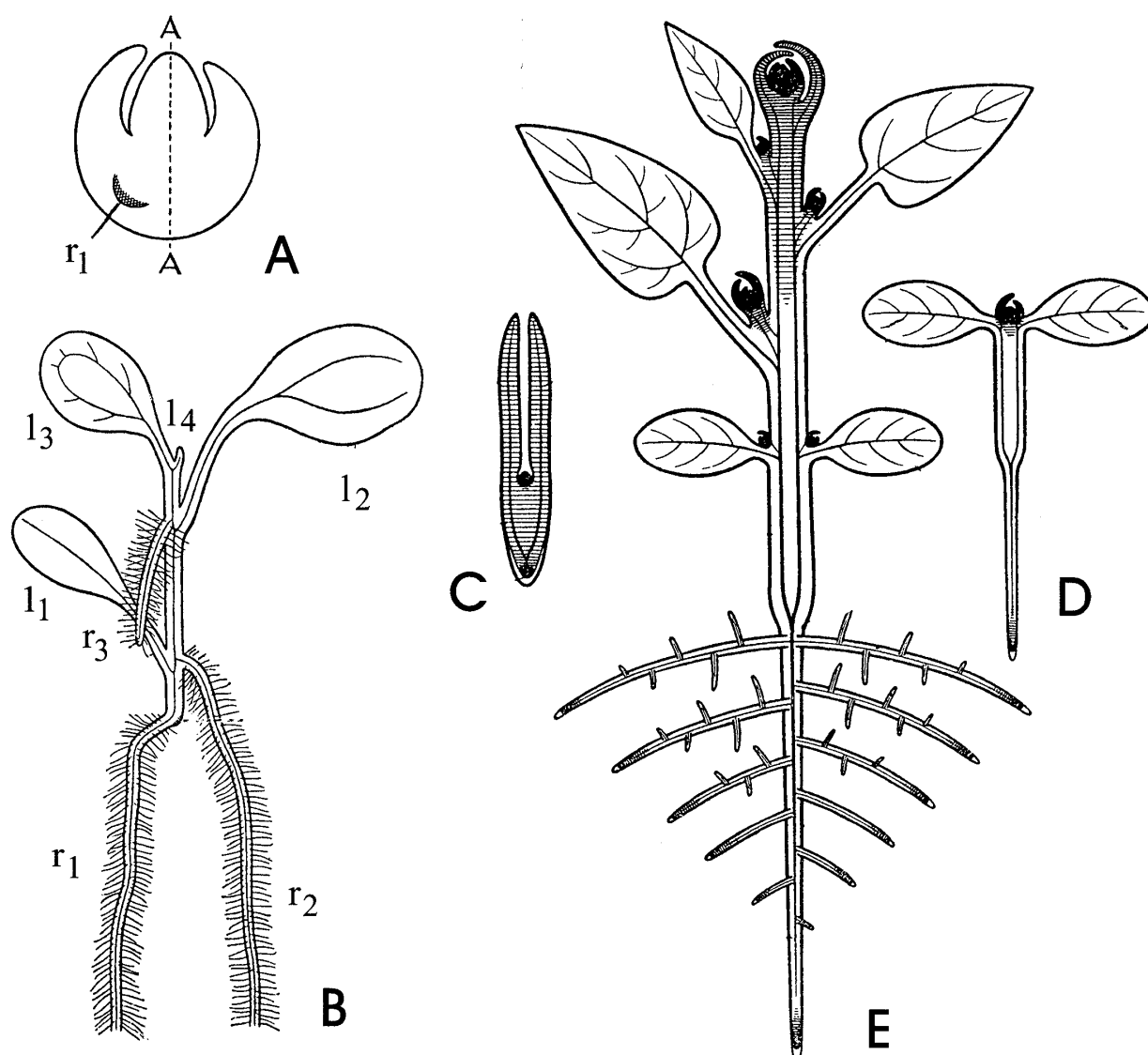


FIG. 1. Homorhizic and allorhizic organisation. A: Unipolar embryo of *Equisetum* in longitudinal section, with the primordium of the first root r_1 . B: Young plant of *Ceratopteris* with the first three roots r_1 - r_3 , and the first four leaves l_1 - l_4 . C: Bipolar embryo of a seed plant, showing (in black) the shoot and root meristem. D: The same with unfolded cotyledons and elongated hypocotyl and radicle. E: The same, further developed, with axillary branching and a root system. (from Troll 1959)

has been shown by cultivating excised embryos outside their surrounding endosperm [see Schneckenburger (1989) and literature cited therein]. For these contrasting modes of shoot organisation in pteridophytes and seed plants the German morphologist Goebel (1930) coined the terms homorhizy and allorhizy, respectively, and particularly Troll (1937)

emphasised this distinction. The fossil record gives only vague indications of the interrelation between these two modes. Seeds of the pteridosperms and cordaites have hardly ever been found to contain an embryo; it is assumed that its development was delayed after pollination or fertilisation. This may be comparable to the situation in *Ginkgo*, where the

³ The fundamentally bipolar character of the seed plant embryo is rejected by Siegert (1989) because to him the inception of the radicle is endogenous (not exogenous as previously thought) and takes place at a late developmental stage.

pollinated ovule can be detached from the mother plant. The earliest fossil seed containing an embryo is from a Walchian conifer of the Early Permian (Mapes *et al.* 1989) and shows a bipolar embryo embedded in endosperm, surrounded by a seed coat and probably displaying seed dormancy, thus possessing all attributes of a modern seed.

Axillary branching, which is a corollary of seed plant organisation, is not clearly developed among extant pteridophytes. In dorsiventral fern rhizomes (*e.g.*, *Davallia*, *Microgramma*) lateral buds are obliquely displaced and supra-axillary (Hirsch & Kaplan 1974, Croxdale 1976); on the vertical axis of *Botrychium* buds appear supra-axillary. In early seed ferns such as *Calamopitys* and *Lyginopteris* the traces of the axillant leaf were inserted 3-5 nodes below the stele of the axillary branch (heteroaxillary; Galtier & Holmes 1982). Little is known about the roots of seed ferns although some fossils of this group have been recovered with stem-borne roots. Thus it is possible that early seed ferns basically lacked both the bipolar condition and axillary branching and that these attributes gradually originated in the seed fern/cordaitalean lineage during the Carboniferous and that the seed plant bauplan was completed by the Late Carboniferous in conifers and cycads; the Late Carboniferous seed fern *Callistophyton* had eustelic stems with axillary buds or branches at each node (Rothwell 1975).

It has become fashionable to invoke mutations known from *Arabidopsis* as a ready mechanism responsible for character transformations such as changes in polarity. However, most of these mutations produce monsters which, if occurring in the wild, probably immediately would be annihilated by stabilising selection. One should also take into consideration that any transitory stage in evolution always must be viable, as Remane (1952) has emphasised more than half a century ago.

Competition for light: further tree forms

Apart from the appearance of the seed ferns, the great innovations at Early Carboniferous times also included several new lycopsid groups, sphenopsids and ferns and brought about noteworthy architectural diversification. The forest communities of that time, particularly of the Late Carboniferous, harboured many different and partly bizarre tree constructions, the biomechanical construction principles of which have been analysed by Mosbrugger (1990). Preferably the better-drained areas were the domain of seed ferns, which were represented by unbranched trees and scramblers. The tree fern *Psaronius* had a relatively thin axis supported by an excessive mantle of adventitious roots running down the stem, similar to, but more pronounced than in the extant tree ferns of the Dicksoniaceae and Cyatheaceae. In wetland habitats sphenopsid and lycopsid trees of several kinds and fern-like plants were prominent. The coeval calamites were medium-sized clonal trees sprouting from rhizomes; they produced hollow stems almost 0.5 m in diameter; with the shrinking of wetland habitats, they disappeared at the beginning of the Permian. Arborescent lycophytes (*Lepidodendron* and *Sigillaria*) represented the strangest kind of tree form, with periderm as the main support-tissue, reaching thickness of at least 20 cm in some species, being waterproof and decay resistant, and remaining photosynthetic; and with stigmarian rhizomorphs bearing rootlets. Although reaching a height of 40-50 m and being up to 2 m wide at the base, they had only a small amount of wood and lacked any secondary phloem (Eggert & Kanamoto 1977); photosynthate supply to the base of the stems may have been difficult, and it has been suggested that the rootlets on stigmarian rhizomorphs were leaf-homologue and perhaps photosynthetic. Ferns were represented by herbs, vines, and trees, and in the Late Carboniferous tree ferns became very prominent

at the expense of lycophytes, but their dominance lasted only for 6 m ys. It has been argued that the increase of canopy height in the Devonian-Carboniferous was an escape from damage by browsing animals but this, at best, may have been a secondary benefit: competition for light may have been the decisive factor.

Variation of the seed plant theme

Throughout the Carboniferous the germination of microspores was generally at the proximal side either through a triradiate or a monolete structure. However, in the Carboniferous distal germination appeared for the first time independently in the two gymnospermous lines, the cordaites and the pteridosperms. The first record of a pollen tube dates also from a seed fern of the Carboniferous, *Callistophyton* (Rothwell 1972), although it is unknown whether it served as a haustorium or for the transfer of the sperms. With the increase in the extent of continental climates in the Early Permian plant groups such as medullosans, xeromorphic pteridosperms (Gigantopterids) and conifers became more dominant, and at least four different gymnospermous groups, the pteridosperms, cordaites, glossopterids, and Caytoniales, had evolved bisaccate pollen (Chaloner 1976). This shift may reflect increasing drought, and it has been suggested (Wodehouse 1935) that the wing-like bladders functioned as a means for reducing moisture loss from the pollen in the air when they folded over the germinal area. Also the pleated (polyplicate) structure of the pollen body known from numerous Permian bisaccate pollen grains may have been a response to aridity (Traverse 1988), allowing to adapt the size of the pollen grain to local moisture levels in the same way as in the pollen of extant *Ephedra* and *Welwitschia*.

With all these achievements, from the end of the Devonian to present, and over a time span of 370 m ys, reproduction by seeds has been the most successful means of exploiting the dry land sur-

face even under adverse climatic regimes, including aridity and winter cold. Further innovations appeared, such as the spread of reticulate leaf venation, but the interval from Permian to Cretaceous was mainly the time of variation of the gymnosperm theme, with the rise and demise of so many seed fern lineages such as glossopterids and Caytoniales, the cordaites and conifers, and the cycadophytes with the Bennettitales, the latter forshadowing insect pollination, which became so decisive in angiosperm evolution.

Angiosperms: super-flexible seed plants

It is now generally accepted and increasingly documented that the properties of the angiosperms did not evolve simultaneously but accumulated over a long period of time (Sun *et al.* 1998, Dilcher 2000, Stuessy 2004). Many traits have been invoked as decisive for the spread of the angiosperms either singly or in conjunction, such as the closure of the carpel, the improved conductive system, or double fertilization. Yet the most important property in the evolution of the angiosperms may have been the flexibility following from their progenetic developmental system, as expressed in the appearance of herbs, simplified gametophytes, and "cheap" diaspores with a secondary endosperm. This new type of endosperm greatly conserved the metabolic effort of the female gametophyte, because the endosperm was not formed before fertilization had occurred. Its origin may lie in an accidental fertilization of a second egg cell, which has been observed to occur in the basal angiosperms of the ANITA grade, where the four-celled female gametophyte gives rise to a diploid endosperm (Friedman & Williams 2004). This may have been a transitory step to the triploid standard endosperm of the rest of the angiosperms, which it is so strongly conserved. Such properties probably permitted early angiosperms to pass through a herbaceous and perhaps

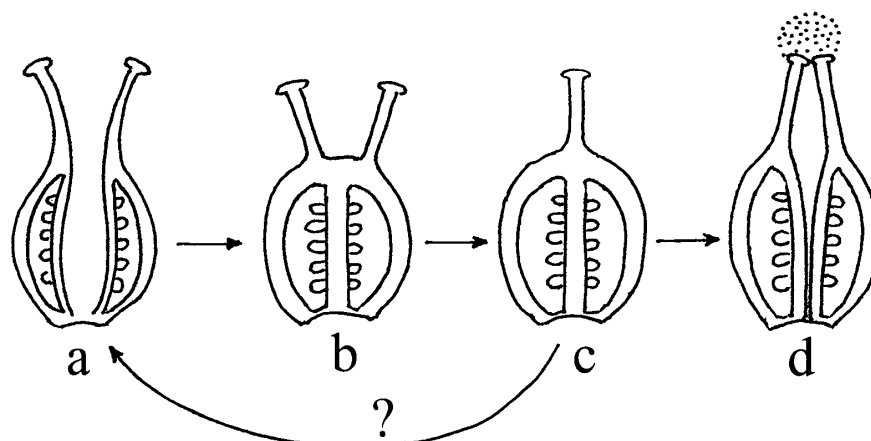


FIG. 2. Character transformations in angiosperm gynoecia. The syncarpous condition (as in b, with distinct stylodia, or in c, with a single style) prevails in angiosperms but sometimes seems to have reverted to a secondarily apocarpous condition (as in d) accompanied by an external compitum; possible reversals to the apocarpous state (as in a) are less well explored.

amphibious stage (Sun *et al.* 1998) and to build-up populations in transient habitats such as flood plains and widening rift valleys.

Early angiosperms probably employed an anthophilous insect fauna inherited from the Bennettitales and perhaps *Caytonia*, consisting of Coleoptera, Diptera, and perhaps moths, whose performance was not only relatively modest but also to some degree may have been destructive. The appearance of Hymenoptera as pollinators in the Late Cretaceous drastically changed the efficiency of insect pollination and led to a successful coevolution among plants and insects. Angiosperm flowers underwent changes in floral structure from actinomorphic to zygomorphic and from polyandrous to oligandrous, with increasingly specialised pollination systems culminating in the highly coadapted tubular and lip flowers as in orchids and asterids. All asterids (corresponding to the former Sympetalae) have "cheap" unitegmic ovules, and most of them are herbaceous, herein perhaps reverting to angiospermous beginnings.

One widespread advance in the angiosperm flower is the one from apocarpy to syncarpy and the acquisition of a single style (Fig. 2) implying an

advantage in terms of increased selection of male gametophytes (Endress 1982); the latter stage being arrived at in about 80 % of angiosperm species. Reversals of this trend in families such as Staphyleaceae, Malvaceae, Apocynaceae and Rutaceae have been revealed to be accompanied by measures for compensating for the loss of the pollen-tube distributing compitum (Endress *et al.* 1983). In other instances, apocarpous flowers occur in eudicot orders or families such as in higher Saxifragales, Crossosomatales, Surianaceae, Quillajaceae, Leguminosae, many Oxalidales and Rosaceae, most of which are embedded in syncarpous groups; they do not show the secondarily acquired compitum mentioned above. In *Paeonia*, for instance, which has been recovered as closely related to the syncarpous Peridiscaceae (Davis & Chase 2004), apocarpy, if correctly interpreted as secondary, may be related to a specialised seed dispersal system implying presentation of seeds on the margins of the follicles.

Yet all this flexibility in angiosperm floral structure was imprinted upon an deeply engraved bauplan of the flower, in which the androecium and the gynoecium are invariably arranged in acropetalous

sequence (the triuridaceous *Lacandonia* being the only known exception), a pattern already known from hermaphroditic Bennettitales.

How far evolutionary success is predictable?

Systematic studies have revealed the strange fact that sister groups can differ strongly in number of their taxa, and this experience long known to taxonomists has been underpinned by the results of numerous molecular studies (e.g., Davies *et al.* 2004). Examples include *Acorus* as sister to all monocots, *Ceratophyllum* sister to all eudicots, *Thurnia* sister to Cyperaceae/Juncaceae, and Barnadesioideae (9 genera/91 spp.) sister to all remaining Compositae (1,400 genera/25,000 spp.). Attempts to explain these discrepancies have failed, and consistent differences in life history traits between these unequal sister groups could not be ascertained. It seems that evolutionary success depends not solely on so-called major advances or key innovations but rather on the coincidence between interactive traits accumulated in a lineage over long periods and a benign constellation of environmental opportunities.

Altogether, the conventional model of evolution of a plant group, implying a slow phase of establishment followed by a burst, and later by a period of dominance, and finally by decline, ignores the role of a changing abiotic and biotic environment. Changes in tectonic activity, atmospheric CO₂ content and global temperature, but also environmental changes brought forth by the biota themselves often provide new evolutionary opportunities. This is exemplified by the rise of the vegetation in the Devonian-Carboniferous. Another example is the origin of the equatorial rain forest, which in the Late Cretaceous first appeared in low palaeolatitudes on both sides of the Atlantic, a region that until then had been localized in the semidry zone of eastern trade winds (Kubitzki & Krutzsch 1996).

The increasing evapotranspiration rates of the equatorial vegetation belt nourished the equatorial rainfall and contributed to the build-up of a fully humid tropical westwind zone, in which a major part of the precipitation is contributed by the evapotranspiration of the forest itself. In comparison with the pre-existing gymnospermous woodlands and palm savannahs these newly originated communities offered enormous evolutionary opportunities for plants and animals and eventually comprised spatially far more complex and more humid habitats than before existed. For instance, whereas Mesozoic fern families had greatly diminished in the Early and Middle Cretaceous (see Collinson 1996), in the Late Cretaceous higher filicalean ferns started to diversify, in the words of Crane (1987) both figuratively and literally in the shadow of the angiosperms (Schneider *et al.* 2004), and an ancient lineage of epiphytic Lycopodiums also entered into a new phase of diversification (Wikström & Kenrick 2001). With such insights we are approaching a broader, more holistic view in which the evolutionary process is embedded in a scenario of a continually changing environment.

The author is most grateful to J.W. Kadereit and J. Rohwer for providing interesting information and critically going through the manuscript.

References

- Bateman, R. M. & W. A. DiMichele. 1994. Heterospory: the most iterative key innovation in the evolutionary history of the plant kingdom. *Biol. Rev.* 69: 345-417.
- Brundrett, M. C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytol.* 154: 275-304.
- Chaloner, W. 1976. In: Ferguson, I. K. & J. Muller (eds.) *The Evolutionary Significance of the Exine*. pp. 1-14. Academic Press, London.
- Collinson, M. E. 1996. "What use are fossil ferns?" - 20 years on with a review of the fossil history of extant pteridophyte families and genera, pp. 349-394. In: Camus, J. M., M. Gibby & R. J. Johns. (eds.) *Pteridology in Perspective*. Royal Botanic Gardens, Kew.

- Crane, P. R. 1987. In: Friis, E. M., W. G. Chaloner & P. R. Crane. (eds.) *The Origins of Angiosperms and their Biological Consequences*. pp. 107-144. Cambridge University Press, Cambridge.
- Croxdale, J. D. 1976. Origin and early morphogenesis of lateral buds in the fern genus *Davallia*. *Amer. J. Bot.* 63: 226-238.
- Davis, C. C. & M. W. Chase. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. *Amer. J. Bot.* 91: 262-273.
- Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis & V. Savolainen. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proc. Natl. Acad. Sci.* 101: 1904-1909.
- Dilcher, D. 2000. Toward a new synthesis: Major evolutionary trends in the angiosperm fossil record. *Proc. Natl. Acad. Sci.* 97: 7030-7036.
- Edwards, D. 2001. *Pinnatiramosus*, a landoverly vascular plant? Abstract, electronically published in "The 12th Plant Taphonomy Meeting, Altlengbach, 26 Oct 2001".
- Eggert, D. A. & N. Y. Kanamoto. 1977. Stem phloem of a Middle Pennsylvanian *Lepidodendron*. *Bot. Gaz.* 138: 102-111.
- Endress, P. K. 1982. Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive angiosperms. *Taxon* 31: 48-52.
- , M. Jenny & M. E. Fallen. 1983. Convergent elaboration of apocarpous gynoecia in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). *Nord. J. Bot.* 3: 293-300.
- Friedman, W. E. & J. H. Williams. 2004. Developmental evolution of the sexual process in ancient flowering plant lineages. *Plant Cell* 16, Suppl. 2004: S119-S132.
- Galtier, J. & J. C. Holmes. 1982. New observations on the branching of Carboniferous ferns and pteridosperms. *Ann. Bot.* 49: 737-746.
- Geng Bao-yin 1986. Anatomy and morphology of *Pinnatiramosus*, a new plant from the Middle Silurian (Wenlockian) of China. *Acta Bot. Sin.* 28: 664-670.
- Goebel, K. 1930. *Organographie der Pflanzen*. 2nd part. 3rd ed. Fischer, Jena.
- Hirsch, A. M. & D. R. Kaplan. 1974. Organography, branching, and the problem of leaves versus bud differentiation in the vining epiphytic fern genus *Microgramma*. *Amer. J. Bot.* 61: 217-229.
- Kato, M. 1988. The phylogenetic relationships of Ophioglossaceae. *Taxon* 37: 381-386.
- Kenrick, P. & P. R. Crane. 1997. *The origin and early evolution of land plants: a cladistic study*. Smithsonian Institution Press, Washington, DC.
- Kubitzki, K. & W. Krutzsch. 1996. Origins of east and south east Asian plant diversity, pp. 56-70. In: Zhang, A. & S. Wu. (eds.). *Floristic Characteristics and Diversity of East Asian Plants*. China Higher Education Press, Beijing and Springer, Berlin.
- Mapes, G., G. W. Rothwell & M. T. Haworth. 1989. Evolution of seed dormancy. *Nature* 337: 645-646.
- Markham, K. R. & J. L. Porter. 1969. Flavonoids in the green algae. *Phytochemistry* 8: 1777-1781.
- Meyer-Berthaud, B., S. E. Scheckler & J. Wendt. 1999. *Archaeopteris* is the earliest known modern tree. *Nature* 398: 700-701.
- Mosbrugger, V. 1990. The tree habit in land plants. *Lecture Notes in Earth Sciences* no 28. Springer, Berlin.
- Remane, A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Geest & Portig, Leipzig.
- Rothwell, G. W. 1972. Evidence of pollen tubes in Paleozoic pteridosperms. *Science* 175: 772-774.
- . 1975. The Callistophytaceae (Pteridospermopsida): I. Vegetative features. *Palaeontographica B*, 151: 171-196.
- Schneckenburger, S. 1989. Studien zur Embryogenese und Keimung verschiedener Gymnospermen unter besonderer Berücksichtigung der Suspensorbildung und Keimwurzelgenese. *Palmarum Hort. Francofort.* 1. 123 pp. Palmengarten, Frankfurt.
- Schneider, H., K. M. Pryer, R. Cranfill, A. R. Smith & P. G. Wolf. 2002. Evolution of vascular plant body plans: a phylogenetic perspective, pp. 330-364. In: Cronk, Q. C. B., Bateman, R. M. & Hawkins, J. A. (eds.). *Developmental Genetics and Plant Evolution*. Taylor and Francis, London.
- , E. Schuettpelz, K. M. Pryer, R. M. Cranfill & R. Lupia. 2004. Ferns diversified in the shadow of angiosperms. *Nature* 428: 553-557.
- Siebert, A. 1989. Zur Phylogenie der Wurzel - ein morphologischer Versuch. Teil I. Die Radicula. Koeltz, Koenigstein.
- Stuessy, T. F. 2004. A transitional-combinational theory for the origin of angiosperms. *Taxon* 53: 3-16.
- Sun, G., D. L. Dilcher, S. Zheng & Z. Zhou. 1998. In search of the first flower: A Jurassic angiosperm,

- Archaeofructus*, from northeast China. *Science* 282: 1692-1695.
- Traverse, A. 1988. Plant evolution dances to a different beat. Plant and animal evolutionary mechanisms compared. *Hist. Biol.* 1: 277-301.
- Troll, W. 1937. *Vergleichende Morphologie der höheren Pflanzen*. Vol. 1. Borntraeger, Berlin.
- . 1959. *Allgemeine Botanik*. 3rd ed. Enke, Stuttgart.
- Raubeson, L. A. & R. K. Jansen. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. *Science* 255: 1697-1699.
- Wikström, N. & P. Kenrick. 2001. Evolution of Lycopodiaceae (Lycopsida): Estimating divergence times from *rcbL* gene sequences by use of nonparametric rate smoothing. *Mol. Phylogen. Evol.* 19: 177-186.
- Wilkinson, D. M. 2001. Mycorrhizal evolution. *Trends Ecol. Evol.* 16: 64-65.
- Wodehouse, R. P. 1935. *Pollen Grains*. McGraw-Hill, New York.

Received August 31, 2004; accepted September 28, 2004